The neural correlates of intentional control

Motivational effects and functional organization

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Zusammenfassung

Intentionale Kontrolle ist ein fundamentaler Aspekt menschlichen Verhaltens. Jedoch gibt es bei der neuronalen Basis solcher Kontrollprozesse noch immer viele offene Fragen. Bis heute bleibt beispielsweise umstritten wie das frontoparietale Intentions-Netzwerk organisiert ist. Weiterhin üben motivationale Prozesse einen großen Einfluss auf intentionale Kontrollprozesse aus. In früheren Studien wurden motivationale und intentionale Kontrollprozesse jedoch oft als unabhängige Funktionen verstanden und untersucht. Diese Dissertation untersucht die neuronalen Grundlagen intentionaler Kontrolle, vor allem auf den Einfluss zweier motivationaler Variablen (Aufgabenschwierigkeit, monetäre Belohnungen) und die funktionelle Organisation des Kontrollnetzwerkes fokussierend. Experiment 1 untersuchte Effekte motivationaler Prozesse auf volitionales Verhalten sowie die neuronale Grundlage dieser Effekte. Experiment 2 untersuchte welche Hirnregionen Verhalten mit seinen Konsequenzen assoziiert. Dies ist eine zentrale Funktion, möchte man die positiven Konsequenzen eigenen Verhaltens maximieren. Experiment 3 untersuchte direkt die Repräsentationen frei gewählter und extern determinierter Intentionen und somit auch die funktionale Architektur des intentionalen Kontrollnetzwerkes. Die Ergebnisse aller drei Studien betonen die Wichtigkeit des anterioren zingulären Kortex, dorsomedialen Präfrontalkortex und des parietalen Kortex für die Vermittlung motivationaler Effekte auf intentionale Kontrolle. Weiterhin deuten die Ergebnisse darauf hin, dass das frontoparietale Kontrollnetzwerk sowohl für die Kontrolle frei gewählten als auch extern determinierten Verhaltens wichtig ist. Diese Ergebnisse stellen einen wichtigen Beitrag für aktuelle Debatten über die neuronale Grundlage intentionalen Verhaltens dar, und erweitern aktuelle Theorien über motivationale und intentionale Kontrolle.

Abstract

Freely choosing one's own course of action is a fundamental aspect of human behavior. Yet, despite its importance, there remain many open questions about the neural basis underlying intentional control of action. On the one hand, the functional organization of the fronto-parietal brain network associated with intentional control remains a debated topic. On the other hand, motivational processes evidently affect intentional control, as we often choose actions which promise desirable outcomes. Despite this, previous research largely treated intentional and motivational control as two independent functions. This thesis aims at shedding light on the neural basis of intentional control, focusing on the effects of two motivational variables on intentional control processes (effort, monetary rewards), as well as the functional organization of the intentional control network. Experiment 1 investigated the effect of motivational processes on voluntary behavior and its neural basis. Experiment 2 assessed which brain regions associate behaviors with their outcomes, an important piece of information for choosing actions which lead the most desirable outcomes. Experiment 3 directly contrasted the representations of freely chosen and externally cued intentions, in this way investigating the functional organization of the intentional control network. Overall, results from those three experiments highlight the role of the dorsal anterior cingulate, dorso-medial prefrontal, and parietal cortex in mediating motivational effects on intentional control. They further suggest that the fronto-parietal intentional control network likely has a role in both controlling behavior that is freely chosen and externally cued. These results inform debates on the neural basis of intentional control and extend some recent theories of motivational and intentional control functions. They provide a promising starting point for a systematic investigation of the neural basis of intentional control.

Abbreviations

AI/FO	Anterior Insula / Frontal Operculum
BOLD	Blood Oxygen-Level Dependent
dACC	Dorsal Anterior Cingulate Cortex
dmPFC	Dorso-Medial Prefrontal Cortex
dlPFC	Dorso-Lateral Prefrontal Cortex
EVC	Expected Value of Control
fMRI	Functional Magnetic Resonance Imaging
GLM	General Linear Model
HRF	Haemodynamic Response Function
MD	Multiple Demand
MVPA	Multivoxel Pattern Analysis
SMA	Supplementary Motor Area
vlPFC	Ventro-Lateral Prefrontal Cortex
WWW	What When Whether Theory of Intentional Action

1 Introduction

"*Finally, modern neuroscience is shifting towards a view of voluntary action being based on specific brain processes, rather than being a transcendental feature of human nature. This will have important ethical implications for the interactions between brain science and wider society, and will inform discussion at the societal level about individual responsibility.*"

Patrick Haggard, 2008 (p. 944)

1.1 General Overview

Flexibly adapting to changing environmental conditions in order to pursue a desired goal is central to human behavior (Miller & Cohen, 2001; Miyake, 2000; Shallice & Burgess, 1991). This ability rests on *intentional control* of behavior, which includes the voluntary formation, maintenance, and implementation of goals or intentions (Brass, Lynn, Demanet, & Rigoni, 2013; Braver, 2012; Koechlin, 2003; Krieghoff, Waszak, Prinz, & Brass, 2011; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). This ability further rests on *motivational control*, which includes associating actions with their outcomes and selecting actions in order to experience positive, and avert negative events (Bromberg-Martin, Matsumoto, & Hikosaka, 2010; Cools, 2008; Schultz, 2006). These two concepts are closely linked, with intentional control describing *what* behavior we choose (Brass & Haggard, 2008), and motivational control describing the reasons *why* we control that behavior (Mars, Sallet, Rushworth, & Yeung, 2011). The interplay of these two processes is intricate and complex, and for a long time, intentional and motivational control processes have been studied largely separately.

Past research on intentional control mainly focused on the representation of tasks and rules (Asaad, Rainer, & Miller, 2000; Forstmann, Brass, Koch, & Cramon, 2005; Goschke & Kuhl, 1993; Reverberi, Gorgen, & Haynes, 2012a, 2012b; Sakai, 2008; Yeung, Nystrom, Aronson, & Cohen, 2006), or the role of consciousness in intentional action (Fried, Mukamel, & Kreiman, 2011; Haggard, 2008; Libet, Gleason, Wright, & Pearl, 1983; Ludwig et al., 2015; Soon, Brass, Heinze, & Haynes, 2008; Soon, He,

Bode, & Haynes, 2013). Previous research on motivational control mainly focused on learning the values of actions and stimuli (Botvinick, 2012; Dayan & Niv, 2008; Shteingart & Loewenstein, 2014) and the role of dopamine in this process (Bromberg-Martin et al., 2010; Jocham, Klein, & Ullsperger, 2011; Schultz, 2002, 2013). Intuitively, stimulus and action values should have an effect on cognitive and intentional control processes, yet their interaction has only begun to receive attention fairly recently (Chiew & Braver, 2011; Doya, 2008; Dreisbach & Fischer, 2012; Gray, Braver, & Raichle, 2002; Jiang & Xu, 2014; Kouneiher, Charron, & Koechlin, 2009; Mars et al., 2011; Pessoa, 2009; Pochon et al., 2002; Shenhav, Botvinick, & Cohen, 2013). This thesis investigates the effects of motivational processes on intentional control, as well as the functional architecture of the intentional control network, using multivoxel pattern analysis (MVPA) of fMRI data (Haynes, 2015).

Previous research has demonstrated that intentional and motivational control processes are implemented in partly overlapping brain networks (Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004; Walton, Croxson, Behrens, Kennerley, & Rushworth, 2007). Intentional and cognitive control (for a definition of both terms see next chapter, p. 12) have often been associated with a fronto-parietal brain network, including the medial prefrontal and dorsal anterior cingulate cortex (dACC, Momennejad & Haynes, 2012; Ridderinkhof, Nieuwenhuis, & Braver, 2007; Ridderinkhof, Ullsperger, et al., 2004; Schuck et al., 2015; Schulz, Bédard, Czarnecki, & Fan, 2011; Shenhav et al., 2013), dorso-lateral prefrontal cortex (dlPFC) and ventro-lateral prefrontal cortex (vlPFC, Badre, Hoffman, Cooney, & D'Esposito, 2009; Braver, 2012; Crowe et al., 2013; Derrfuss, Brass, & Yves von Cramon, 2004; Koechlin, 2003; Miller & Cohen, 2001; Reverberi et al., 2012b; Stokes et al., 2013), and parietal cortex (Brass, Ullsperger, Knoesche, Von Cramon, & Phillips, 2005; Esterman, Chiu, Tamber-Rosenau, & Yantis, 2009; Shomstein, 2012). Motivational control has mainly been associated with the striatum (Balleine & Ostlund, 2007; Delgado, 2007; Harsay, Cohen, Reneman, & Ridderinkhof, 2011; Kahnt, Park, Burke, & Tobler, 2012; O'Doherty, 2004) and orbitofrontal / ventro-medial prefrontal cortex (Kahnt, Chang, Park, Heinzle, & Haynes, 2012; Kahnt, Heinzle, Park, & Haynes, 2010; Klein-Flügge, Barron, Brodersen, Dolan, & Behrens, 2013; O'Doherty, Kringelbach,

Rolls, Hornak, & Andrews, 2001; Padoa-Schioppa & Assad, 2006; Sescousse, Redoute, & Dreher, 2010; Wallis, 2007). Although most research focuses on these two brain regions, it has been shown that the dACC (Behrens, Woolrich, Walton, & Rushworth, 2007; Camille, Tsuchida, & Fellows, 2011; Hughes & Beer, 2012; Kennerley, Behrens, & Wallis, 2011; Rushworth, Behrens, Rudebeck, & Walton, 2007) and parietal cortex (Dorris & Glimcher, 2004; Kahnt, Park, Haynes, & Tobler, 2014; Koch et al., 2008; Peck, Jangraw, Suzuki, Efem, & Gottlieb, 2009; Sugrue, 2004) might also play a role in motivational control, mainly being associated with the representation of action values. The intentional and motivational control networks are thus overlapping in the dACC and parietal cortex, which might mediate interactions between these two networks (Chiew & Braver, 2011; Doya, 2008; Goschke & Bolte, 2014; Holroyd & Yeung, 2012; Kouneiher et al., 2009; Montague, Hyman, & Cohen, 2004; Shenhav et al., 2013). Other regions possibly mediating motivational effects on control functions include the lateral PFC (O'Connor, Upton, Moore, & Hester, 2015) and the striatum (Fallon & Cools, 2014). In this thesis, two different motivational variables are investigated, monetary rewards and effort, with both having potentially different effects on control processes (Paschke et al., 2015)[1]. Although monetary rewards have been used more often than effort in previous experiments as a motivational variable (e.g. Kleinsorge & Rinkenauer, 2012; Williams, Bush, Rauch, Cosgrove, & Eskandar, 2004), effort and difficulty have also been shown to motivate behavior (Botvinick, Huffstetler, & McGuire, 2009; Crittenden & Duncan, 2014; Croxson, Walton, O'Reilly, Behrens, & Rushworth, 2009).

One open question is whether any of these brain regions are also involved in mediating motivational effects on *freely chosen* behavior. To date, previous research has mostly investigated motivational effects on *externally cued* behavior (Chiew & Braver, 2014; Kleinsorge & Rinkenauer, 2012; Locke & Braver, 2008; Müller et al., 2007), for instance cueing subjects to switch between different tasks and assessing the effect of reward on that process (Jiang & Xu, 2014). However, voluntarily choosing

[1] Other motivational variables, which are not directly investigated in this thesis, include positive and negative affect (Erk et al., 2003; Goschke & Bolte, 2014; Pessoa, 2009) or primary rewards (Beck, Locke, Savine, Jimura, & Braver, 2010; Kubanek & Snyder, 2015; McClure, Ericson, Laibson, Loewenstein, & Cohen, 2007) .

one's own action is an integral part of every-day behavior (Arrington & Logan, 2004; Filevich & Haggard, 2012). In order to understand how motivation might affect adaptive and intentional control processes, motivational effects on freely chosen actions need to be investigated. A second open question relates to the functional architecture of the cognitive and intentional control network. There is an ongoing debate about the organization of that network, with some arguing for specific control functions being localized to dissociable brain regions, especially in the lateral PFC (Badre & D'Esposito, 2009; Koechlin, 2003). Others are arguing for functional generality of the control network, with many functions relying on the same control-related brain regions (Duncan, 2010; Fedorenko, Duncan, & Kanwisher, 2013). A clear understanding of the network organization is important for a deeper understanding the neural basis of intentional control.

This thesis contains three experiments that contribute to answering these questions. The first experiment (Wisniewski, Reverberi, Tusche, & Haynes, 2014) investigated the effect of motivational control on freely chosen behavior using MVPA on fMRI data. The second experiment (Wisniewski, Reverberi, Momennejad, Kahnt, & Haynes, 2015) investigated the associations of specific tasks with their rewarding outcomes, which are a key component and a prerequisite for motivational effects on intentional control. The third experiment (Wisniewski, Goschke, & Haynes, 2016) compared the representations of freely chosen and externally cued intentions, investigating whether the intentional control network is functionally specialized with respect to this variable.

The structure of this thesis is as follows. In the remainder of the Introduction chapter, I will first introduce the concept of intentional control. Then, I will describe previous findings on the functional architecture of the brain network underlying intentional control functions. In the last part of the Introduction, I will present previous research on the interaction of motivational and intentional control and highlight open questions in the field. In the Methods chapter, I will first describe the neural basis of fMRI, highlight the difference between univariate and multivariate analysis strategies, and then present findings on the neural basis of MVPA. In the Experiment chapter, a more detailed description of the three experiments of this thesis will be given, before their results will be put into

context in the General Discussion chapter. Special emphasis will be given to how results expand our knowledge of the functional architecture of the intentional control network and how different parts of this network are influenced by motivational control processes. Finally, I will outline future directions of this research, which will further contribute to our understanding on how motivational and intentional control interact to support adaptive control of behavior.

1.2 Intentional control of behavior

1.2.1 Theories of intentional action

In cognitive neuroscience intentional control often describes the voluntary formation, maintenance, and implementation of intentions, and has mainly been operationalized as internally guided behavior, as contrasted with externally guided behavior (Brass et al., 2013; Cunnington, Windischberger, Deecke, & Moser, 2002; Deiber et al., 1991; Forstmann, Brass, Koch, & Von Cramon, 2006; Jahanshahi et al., 1995; Müller et al., 2007; Passingham, Bengtsson, & Lau, 2010). More specifically, externally guided behavior is a direct response to external stimuli, such as imperative instructions (e.g. Monsell, 2003). Internally guided behavior on the other hand is performed in the absence of external stimuli, and is for instance based on abstract urges (Libet et al., 1983), or other "internal cues" such as elapsed time or one's own preceding actions (Schüür & Haggard, 2011). This operationalization of intentional control of behavior allows distinguishing it from the related concept of cognitive control[2]. Whereas intentional control describes the control of internally guided behavior, cognitive control is used as an overarching term describing the control of both internally and external guided behavior (Brass et al., 2013; Miller & Cohen, 2001). Intentional control is just one of many aspect of cognitive control. While other research focuses on e.g. reactive vs. proactive control processes (Braver, 2012), or transient vs. sustained control processes (Dosenbach et al., 2007), this

[2] Cognitive control is the set of functions which "permit selection of actions that are consistent with our goals and context." (Badre, 2008).

thesis investigates intentional control processes in more detail. Despite its wide use in experimental research, operationalizing intentional control in terms of internally vs. externally guided behavior is not without problems (Nachev & Hacker, 2014). Not only is it difficult to clearly separate external and internal influences on behavior, but also to directly assess the influence of internal determinants on behavior (Nachev & Husain, 2010; Schüür & Haggard, 2011). Still, contrasting internally and externally guided behavior can be a useful tool and approximation to begin the empirical investigation of the neural basis of intentional control.

One approach to overcome the dichotomous view of internal vs. external determinants of behavior has been proposed by Haggard (2008). Whenever external stimuli provide explicit instructions on which task to perform, subjects only need to determine the appropriate response to the target stimulus. If such clear instructions are missing, subjects additionally need to consider multiple alternative choice options and choose among them. In this light, the amount of information which needs to be generated internally separates internally and externally guided actions. This view goes beyond the internal vs. external dichotomy, by quantifying different degrees of internal information generation. Using this theory, different types of behavior can easily be distinguished, including behavior which is strongly internally guided (Libet et al., 1983; Soon et al., 2008), strongly externally guided (Jiang & Xu, 2014; Monsell, 2003), or combining aspects of both, as is the case in value-based decision-making (Boorman, Behrens, Woolrich, & Rushworth, 2009; Hampton & O'Doherty, 2007).

Further conceptual refinements are provided by the *What-When-Whether (WWW) Model of Intentional Action* (Brass & Haggard, 2008; Haggard, 2008). This theory distinguishes three necessary processing steps for forming and executing an intention. It needs to be decided *whether* to act, *what* action to choose, and *when* to perform that action. These three aspects of intentional action can be localized to partly dissociable brain regions, supporting this conceptual distinction (Brass et al., 2013). *What* decisions seem to be processed in the dACC (Krieghoff et al., 2011), while *when* decisions seem to be processed in the SMA/preSMA (Hoffstaedter, Grefkes, Zilles, & Eickhoff, 2013;

Momennejad & Haynes, 2012; Soon et al., 2008). *Whether* decisions seem to be processed in the dmPFC, located dorsally of the dACC (Brass & Haggard, 2007; Filevich & Haggard, 2012).

Both theories described above have the potential to promote our understanding of intentional action, providing descriptions of the *processes* underlying intentional control. Although cognitive neuroscience is yet far from providing a unifying consensual theory of intentional control, such theories can be used to formulate and test hypotheses about its neural implementation.

1.2.2 Neural correlates of intentional control

The neural basis of intentional control of behavior has been investigated for decades (e.g. Libet et al., 1983; Penfield, 1954; Romo & Schultz, 1987), yet the precise function of the discovered regions remains elusive. Previous research consistently associated a fronto-parietal brain network with *cognitive* control (Cole & Schneider, 2007; Dosenbach et al., 2006; Niendam et al., 2012). This network includes the dACC (Alexander & Brown, 2011; Forstmann et al., 2006; Mansouri, Tanaka, & Buckley, 2009; Shenhav et al., 2013), dmPFC (Brass et al., 2013; Krieghoff et al., 2011), lateral PFC (Bengtsson, Haynes, Sakai, Buckley, & Passingham, 2009; Gilbert, Gollwitzer, Cohen, Oettingen, & Burgess, 2009; Kouneiher et al., 2009; Miller & Cohen, 2001), and parietal cortex (Esterman et al., 2009; Pesaran, Nelson, & Andersen, 2008; Shomstein, 2012). The neural correlates of *intentional* control have often been investigated by directly contrasting brain activity of freely chosen and externally cued behavior (Bengtsson et al., 2009; Cunnington et al., 2002; Forstmann et al., 2006; Jahanshahi et al., 1995; Müller et al., 2007; Zhang, Kriegeskorte, Carlin, & Rowe, 2013). This contrast identified regions that are highly similar to the fronto-parietal cognitive control network described above (Niendam et al., 2012). The dACC and parietal cortex are more strongly activated during free choice (Forstmann et al., 2006), which seems to suggest that these brain regions are involved in the voluntary selection of behavior. Note however that this might also reflect general preparatory processes, which are correlated with voluntary action. Conflict resolution (Brass et al., 2013) as well

as working memory demands (Lau, Rogers, Ramnani, & Passingham, 2004) are higher during free choice, which might also explain the observed increases in neural activity. This demonstrates that an increase of activity *per se* does not signify that a brain region has intention-specific functions, such as representing the content of an intention.

A method which circumvents this issue and identifies brain regions that are selectively involved in processing intentions is MVPA (Haynes, 2015; Kriegeskorte, 2011). It can be used to test whether distributed spatial activation patterns in the brain contain information about experimental conditions (Haynes & Rees, 2006; Kriegeskorte, Goebel, & Bandettini, 2006, for more information on MVPA see Methods section, p. 24ff.). Previous research demonstrated that MVPA can be used successfully to discriminate multiple different freely chosen (Haynes et al., 2007; Soon et al., 2013; Zhang et al., 2013) or different externally cued conditions (Bode & Haynes, 2009; Gilbert, 2011; Momennejad & Haynes, 2013; Reverberi et al., 2012a; Woolgar, Afshar, Williams, & Rich, 2015; Woolgar, Thompson, Bor, & Duncan, 2011). Through direct comparisons of multiple freely chosen intentions, general preparatory processes are kept constant across conditions as they are similar for different freely chosen intentions. MVPA thus has the capacity to identify intention-specific brain regions, which include the medial and lateral PFC (Haynes et al., 2007; Zhang et al., 2013), parietal cortex (Soon et al., 2013), precuneus and frontopolar cortex (Soon et al., 2008) for freely chosen intentions. Using MVPA, externally cued intentions were found to be encoded in a network including the lateral PFC, parietal cortex, and dACC (Bode & Haynes, 2009; Momennejad & Haynes, 2013; Reverberi et al., 2012b; Woolgar et al., 2011; Zhang et al., 2013). The intentional control network identified using MVPA is similar to the control network identified using univariate methods, confirming that these brain regions have intention-specific functions.

1.3 Functional organization of the intentional control network

Although the brain regions constituting the intentional control network are mostly known, the functional organization of these regions remains unclear. Are parts of the network functionally specialized, for instance being only involved in processing freely chosen as opposed to externally cued intentions? Or do the brain regions constituting the intentional control network have a more general role in processing intentional actions? Most theories on the functional organization of the fronto-parietal cortex do not specifically address intentional control, but more broadly address cognitive control. As intentional control is part of the cognitive control concept (Brass et al., 2013), these theories remain relevant for intentional control as well. They can be broadly divided into those in favor of functional specialization (Badre & D'Esposito, 2009; Dosenbach et al., 2007; Koechlin & Summerfield, 2007) and those in favor of functional generality (Cole et al., 2013; Duncan, 2010).

Functional specialization seems to be most evident along the lateral PFC, which has been proposed to be organized along an anterior to posterior gradient (Badre & D'Esposito, 2009; Koechlin, 2003). The anterior parts of the lateral PFC seem to be associated with processing highly abstract task rules, while the posterior parts of the lateral PFC seem to be associated with concrete action-related task rules (Badre & D'Esposito, 2009; Nee & Brown, 2012). Alternatively, it has been proposed that sustained control is correlated with activity in the anterior lateral PFC, while transient control processes are correlated with posterior parts of the lateral PFC (Koechlin, 2003). Interestingly, similar gradient theories have been proposed for motivational control processes along the medial PFC (Kouneiher et al., 2009; Venkatraman, Rosati, Taren, & Huettel, 2009). Although such gradient theories describe the organization of the PFC, they make no predictions about other parts of the control network, such as the parietal cortex. At the level of the whole network, it has been proposed that the cognitive control network can be sub-divided into two separate sub-networks (Dosenbach et al., 2007). In their paper, Dosenbach et al. (2007) argue that a fronto-parietal sub-network, including the parietal cortex, precuneus, and dlPFC provides flexible trial-by-trial control in response to

feedback, such as error-related control adjustments (Botvinick, Braver, Barch, Carter, & Cohen, 2001). A cingulo-opercular sub-network, including the anterior insula/frontal operculum (AI/FO), dACC, and frontopolar cortex provides across-trial stable control signals, such as the maintenance of task sets (Braver, 2012). This theory is partly compatible with gradient theories of PFC function, in that the anterior PFC is associated with sustained control, while the posterior PFC is associated with transient control.

In contrast to theories of functional specialization, alternative accounts emphasize the generality of frontal and parietal cortex functions (Cole et al., 2013; Dehaene, Kerszberg, & Changeux, 1998; Duncan, 2010). Specifically, it is though that a network including the lateral PFC, dACC, SMA, AI/FO, and parietal cortex contain neuronal populations which are highly flexible and are able to adapt to a wide range of different task demands, showing no strong functional specialization. These brain regions are sometimes called the multiple demand (MD) network and have been shown to be involved in the processing of a wide range of complex behaviors involving e.g. mental arithmetic, working memory, or suppressing irrelevant information (Fedorenko et al., 2013). This network further flexibly connects to other networks, e.g. motor, auditory, or attentional networks, depending on the current task demands (Cole et al., 2013). Importantly, the MD network has been shown to encode externally cued task rules, with representations being flexibly adapted to different environmental demands, such as task difficulty (Woolgar et al., 2015), or control demands (Waskom, Kumaran, Gordon, Rissman, & Wagner, 2014). Although apparently contradictory, these two opposing views are not mutually exclusive. It is conceivable that the MD network indeed has highly general functions, while other regions outside of the MD network remain more strongly functionally specialized.

Very few theories directly describe the functional architecture of the intentional control network, possibly because intentional control is thought of as being a part of cognitive control already. Two theories on intentional control emphasize functional specialization within the network, as is the case in the WWW theory of intentional action (Brass & Haggard, 2008). As stated above (p. 13f.), the

WWW theory draws support from the fact that the three aspects of intentional action can be localized to distinct parts of the medial PFC (Brass et al., 2013). A related and compatible theory focuses on the difference between freely chosen and externally cued intentions. Some evidence suggests that the medial PFC is mainly correlated with freely chosen intentions (Brass & Haggard, 2008; Brass et al., 2013; Cunnington et al., 2002; Jahanshahi et al., 1995; Mueller, Brass, Waszak, & Prinz, 2007; Passingham et al., 2010), while the lateral PFC is mainly correlated with externally cued intentions (Bode & Haynes, 2009; Forstmann et al., 2005; Reverberi et al., 2012a, 2012b). Note however that other results find no support for a medial vs. lateral dissociation (Haynes et al., 2007; Momennejad & Haynes, 2013), show a dissociation only within the lateral PFC (Zhang et al., 2013), or provide evidence for a dissociation in the opposite direction (Gilbert et al., 2009).

Evidently, theories on the functional organization of the intentional control network are far from consensual and further evidence is needed. In recent years, a growing number of fMRI studies using MVPA to identify brain regions specialized in representing free or cued intentions have been presented, with mixed results (Bode & Haynes, 2009; Hampton & O'Doherty, 2007; Haynes et al., 2007; Momennejad & Haynes, 2012; Soon et al., 2008). This might partly be due to the fact that these studies often investigated either only freely chosen intentions (Soon et al., 2008, 2013) or only externally cued intentions (Bode & Haynes, 2009; Waskom et al., 2014). A comparison of their results thus confounds the difference between free and cued intentions with differences in experimental design parameters, such as the specific tasks that were used. This might contribute to the heterogeneous findings in the literature. In order to assess possible differences between representations of free and cued intentions, both need to be studied using the same tasks, ideally comparing their representations within subjects. Such studies are still rare (Zhang et al., 2013), and therefore the functional organization of the intentional control network remains an open question.

1.4 Motivational influences on intentional control

Goal-directed adaptive control of behavior rests critically on motivational control, since goal states intrinsically imply a motivation to reach them (Miller, Shankar, Knutson, & McClure, 2014). The concept of motivational control describes the learning of stimulus and action values (Mars et al., 2011), as well as adjustment of behavior to maximize action outcomes (Montague et al., 2004). Most often monetary rewards are used to study motivational control (Daw, Gershman, Seymour, Dayan, & Dolan, 2011; Schultz, 2013; Wallis, 2013). However, effort and difficulty can also be used to investigate motivational control (Botvinick et al., 2009; McGuire & Botvinick, 2010). In this thesis both the effect of reward and effort on control processes will be investigated. Brain regions associated with motivational control include the striatum (Schultz, 2013; Tanaka et al., 2004), which is thought to compute the difference between the expected and actual outcomes of actions, a signal which is then used to adjust behavior (Bayer & Glimcher, 2005; Daw et al., 2011; Kahnt, Park, et al., 2012; Soltani & Wang, 2008). Furthermore, while the orbitofrontal cortex is thought to represent subjective *stimulus* values (Kahnt et al., 2010; Klein-Flügge et al., 2013; Tremblay & Schultz, 2000; Wallis, 2007), the dACC is widely believed to represent the subjective value of *actions* (Camille et al., 2011; Kennerley et al., 2011; Rushworth, Behrens, et al., 2007). Although generally not considered a core region for motivational control, the parietal cortex has also been suggested to represent action values (Platt & Glimcher, 1999; Sugrue, 2004). The motivational control network thus partly overlaps with the intentional control network, especially in the dACC and parietal cortex, making these regions prime candidates for mediating motivational effects on intentional control processes.

Motivational control can principally affect intentional control in two ways, either by driving the formation of an intention (‘Wanting to do X’; e.g. Ballard & Knutson, 2009; Doya, 2008), or by affecting its implementation and execution (‘Wanting to perform well’; e.g. Hayden et al., 2011; Koch et al., 2008). The interaction of motivational and cognitive control has received increased attention in recent years (Cools, 2008; Doya, 2008; Dreisbach & Fischer, 2012; Frank, 2011; Kouneiher et al.,

2009; Müller et al., 2007; Pochon et al., 2002), showing that many well established cognitive control functions are modulated by motivational processes. For instance, switching between different tasks is an effortful process which requires cognitive control and can be observed in increased reaction times (RTs) immediately after task switches (Monsell, 2003). Recent studies demonstrated that the prospect of earning a reward reduces the RT costs associated with switching between tasks (Kleinsorge & Rinkenauer, 2012), demonstrating that rewards can increase the effectiveness of cognitive control. This effect is possibly due to enhanced backward inhibition of task sets performed in the past (Jiang & Xu, 2014), and mediated by the vlPFC and ventral striatum (Avila et al., 2012; see also Etzel, Cole, Zacks, Kay, & Braver, 2015). Other control functions that have been found to be modulated by rewards include working memory (Fallon & Cools, 2014; Taylor et al., 2004), inhibition and self-control (Boehler, Hopf, Stoppel, & Krebs, 2012; O'Connor et al., 2015), and conflict resolution (Dreisbach & Fischer, 2012; Etzel et al., 2015). Taken together, these results suggest that many control functions are affected and enhanced by motivational processes, and that these interactions are mediated by brain regions that are part of either the cognitive or motivational control network.

Theories of intentional action rarely incorporate motivational control parameters explicitly. As the name suggests, the WWW theory of intentional action distinguishes *what*, *when*, and *whether*, but has no *why* aspect of intentional action. Yet, previous findings suggests that rewards affect choices of motor actions (Hayden et al., 2011; Shima & Tanji, 1998; Sugrue, 2004) and tasks (Boorman et al., 2009; Hampton & O'Doherty, 2007), demonstrating that *what* choices are indeed subject to motivational effects. Some initial work further suggests that *whether* choices are also affected by rewards (Boehler et al., 2012).

A key region often implicated in mediating motivational effects on cognitive control is the dACC (Bush et al., 2002; Holroyd & Yeung, 2012; Kennerley, Walton, Behrens, Buckley, & Rushworth, 2006; Rushworth, Behrens, et al., 2007; Walton et al., 2007). The dACC is both part of the cognitive control network (Dosenbach et al., 2007; Ridderinkhof, Ullsperger, et al., 2004), as well as motivational

control network (Rushworth & Behrens, 2008). In the *expected value of control* (EVC) theory (Shenhav et al., 2013), the key role of the dACC is explained in terms of a cost-benefit analysis. The EVC theory suggests that the dACC integrates the potential rewards and costs associated with control-demanding behavior. It weighs the potential gain (Knutson, 2005) with the cost of exerting effortful control over a task (McGuire & Botvinick, 2010), calculating its net benefit for the agent. In this light, the role of the dACC is to integrate motivationally relevant information into cognitive control processes, explaining its key role in both motivational and cognitive control. Additionally, the dACC is ideally connected to other brain regions in order to perform this computation (Pessoa, 2009, 2010). It receives inputs from the motivational control network (Rushworth, Buckley, Behrens, Walton, & Bannerman, 2007) and sends outputs to the lateral PFC to implement control (Pessoa, 2009).

The parietal cortex also is a candidate region for mediating motivational effects on cognitive control functions, yet it received relatively little attention in this context. On the one hand the parietal cortex plays an important role in cognitive control (Crowe et al., 2013; Esterman et al., 2009; Shomstein, 2012), especially in representing task-sets (Bode & Haynes, 2009; Reverberi et al., 2012b; Waskom et al., 2014). In addition, the parietal cortex also plays a role in motivational control (Kahnt et al., 2014; Peck et al., 2009), representing action values (Kubanek & Snyder, 2015; Louie, Grattan, & Glimcher, 2011; Sugrue, 2004). Some recent evidence suggests that task-set representation in the parietal cortex are indeed influenced by rewards (Etzel et al., 2015), as well as effort (Woolgar et al., 2015). Although the majority of the work points to the dACC in mediating motivational effects on control functions, this recent evidence suggests that the parietal cortex might play a similar role.

Despite the growing understanding of motivational effects on cognitive control, several open questions remain. First, the vast majority of previous experiments investigated motivational effects on externally cued behavior (e.g. Etzel et al., 2015; Kleinsorge & Rinkenauer, 2012; Woolgar et al., 2015). It remains unclear whether and how representations of freely chosen intentions are affected by motivational control processes.

Second, previous studies on freely chosen intentions largely fail to investigate the influence of motivational control processes (Forstmann et al., 2006; Libet et al., 1983; Soon et al., 2008). This has led some researches to question whether these experiments fully capture intentional control processes as they occur in real-life situations (Baumeister, 2008; Bode et al., 2014). We mostly choose behavior based on specific reasons, e.g. expecting a favorable outcome. This is in stark contrast to many experiments on intentional control (Forstmann et al., 2006; Libet et al., 1983; Soon et al., 2008), where choice options are highly similar and there is no reason to favor one choice option over the other, forcing subjects to resort to random choices (Ebert & Wegner, 2011). Therefore, making choice options more different through the use of e.g. rewards or effort will arguably better approximate behavior observed in real-life situations. Both of these points highlight the need to study motivational effects on intentional control processes, in order to increase the ecological validity of intentional control experiments and to test whether observed effects on externally guided behavior generalize to freely chosen behavior.

Third, a prerequisite for motivational effects on control processes is to first associate intentions with their outcomes. Only after such associations are established, behavior can be adjusted accordingly (Kennerley et al., 2006). The neural basis of these associations remains largely unknown, which is due to the fact that their representations were often confounded with preparatory processes in previous experiments. Associating an intention with a high reward will lead to task preparation and reward expectation processes (Boorman et al., 2009), increase the likelihood of choosing that task (Hampton & O'Doherty, 2007), and enhance control functions (Kleinsorge & Rinkenauer, 2012). In order to investigate the neural basis of intention – outcome associations, their neural signals need to be de-correlated from such confounding preparatory processes first.

1.5 Open questions

In summary, this thesis will address three open questions in the literature on the neural basis of intentional control. Experiment 1 investigated the interaction of motivational control and intentional control processes in a modified effort-based free choice task. This will allow testing whether brain regions that have been implicated in mediating motivational effects on externally cued behavior are also involved in mediating motivational effects on freely chosen behavior. This experiment will further increase the ecological validity of intentional control experiments, by incorporating motivational into intentional control processes, giving subjects clear reasons to choose one option over the other. Experiment 2 investigated the neural correlates of task-reward-associations. Before task performance can be affected by motivational control processes, tasks need to be associated with their outcomes first. The neural correlates of such associations have been elusive in the past, and a modified delayed intention task is presented which circumvents some of the issues of previous work. Experiment 3 compared the representations of freely chosen and externally cued intentions directly within subjects and using the same tasks, in this way investigating the functional organization of the intentional control network.

2 Methods

2.1 Neurobiological basis of fMRI

Functional magnetic resonance imaging (fMRI) is a widely used technique in the cognitive neurosciences (Cabeza & Nyberg, 2000; Yeo et al., 2014), which allows non-invasive measurements of neural responses through the BOLD contrast (Ogawa, Lee, Nayak, & Glynn, 1990)[3]. The BOLD contrast leverages the fact that oxygenated and deoxygenated blood has different magnetic

[3] More details on methodological points not otherwise cited can be found in Huettel, Song, & Mccarthy, 2004 or Ashby, 2011.

properties. While oxygenated blood is diamagnetic, deoxygenated blood is paramagnetic. Whenever neuronal activity increases in a brain region, its metabolic demands lead to a shift in the ratio of oxygenated to deoxygenated blood, which is measured using MRI (Buxton & Frank, 1997; Turner, Le Bihan, Moonen, Despres, & Frank, 1991). The BOLD effect peaks around 3-6 seconds after the onset of neural activity, with some variability between different brain regions (Heeger & Ress, 2002). The sluggishness of the BOLD response in time restricts the interpretation of signal time-courses (but see Glover, 1999; Ollinger, Shulman, & Corbetta, 2001), yet the low temporal resolution is compensated by a comparatively high spatial resolution (Zimmermann et al., 2011). This high spatial resolution is used in MVPA in order to extract information from spatial activation patterns (Haxby et al., 2001; Haynes, 2015; Haynes, Driver, & Rees, 2005; Kamitani & Tong, 2005; Yacoub, Harel, & Uğurbil, 2008). The BOLD effect only reflects metabolic effects and is therefore an indirect measure of neuronal activity, raising the question which aspects of neuronal activity are reflected in the BOLD effect (Logothetis, 2008). Although some evidence suggests that the BOLD effect is more closely related to pre-synaptic activity than neuronal spiking (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001), this issue remains unresolved. Nevertheless, fMRI currently remains one of the most promising non-invasive tools to investigate brain function, and it is widely used in the cognitive neurosciences.

2.2 Univariate vs. multivariate analysis of fMRI data

Today, the most common approach to analyze fMRI data is the *mass-univariate analysis* approach (Ashby, 2011). First, a general linear model (GLM) is used to correlate the acquired BOLD time-series with the time-course of an experimental factor for every individual voxel. Experimental factors are specified in the *design matrix* (Friston et al., 1994) and are typically modeled using boxcar functions convolved with a canonical HRF. The GLM is used to estimate a regression coefficient (*beta*) for each voxel, reflecting how strong the BOLD time-series correlates with the experimental factor. This results in a 3-D map of beta coefficients for the whole brain in each subject. At the group level,

statistical tests are performed on each voxel independently, assessing whether the average regression coefficient across all subjects deviates from zero significantly (for a more detailed discussion see Ashby, 2011). The mass-univariate approach can detect neural correlates of cognitive processes which are reflected in the average signal differences of single voxels (Davis et al., 2014). Information about cognitive processes that is spread across multiple voxels is inaccessible to mass-univariate analyses, limiting its sensitivity.

An alternative approach, multivoxel pattern analysis (MVPA), takes into account the BOLD signals of more than one voxel simultaneously (Haxby, Connolly, & Guntupalli, 2014; Haynes & Rees, 2006; Kriegeskorte et al., 2006). It can thus additionally detect information contained in spatially distributed activation patterns (Haynes, 2015, but see Davis et al., 2014 for more information on the relation between spatial patterns and MVPA results), making MVPA a potentially more sensitive method than mass-univariate analyses (Davis et al., 2014). This increase in sensitivity inadvertently leads to an increased influence of possible confounding variables on the results, which need to be controlled for carefully (Todd, Nystrom, & Cohen, 2013). MVPA has been gaining popularity fast over the last decade, and it has been used successfully to decode the content of visual perception (Kay, Naselaris, Prenger, & Gallant, 2008) and working memory (Christophel, Cichy, Hebart, & Haynes, 2015), cognitive control parameters (Esterman et al., 2009), or task rules (Etzel et al., 2015; Haynes et al., 2007; Reverberi et al., 2012b; Waskom et al., 2014).

One widely used MVPA method is *pattern classification* (Haxby et al., 2014; Haynes, 2015). Here, a classifier is trained to discriminate spatial activation patterns associated with two or more experimental conditions (Haynes & Rees, 2006; Tong & Pratte, 2012). Two of the most common classification algorithms are *support vector machines* and *linear discriminant analyses* (for an introduction and comparison of different classification algorithms see Mur, Bandettini, & Kriegeskorte, 2008; Pereira & Botvinick, 2011). Typically, cross-validation procedures are then used to get an unbiased estimate of generalization performance. This is necessary to avoid problems of overfitting (Kriegeskorte et al., 2006). Given that fMRI datasets are often high-dimensional, MVPA

requires some form of feature selection in order to avoid the curse of dimensionality (Haynes, 2015). The features on which classifiers are trained can be selected e.g. using principal component analysis (Mourão-Miranda, Bokde, Born, Hampel, & Stetter, 2005), or by restricting classifiers spatially into either "searchlights" (Etzel, Zacks, & Braver, 2013; Kriegeskorte et al., 2006), or ROIs (Hampton & O'Doherty, 2007; Waskom et al., 2014). Often, MVPA is applied for each subject independently, and results are then assessed for statistical significance at the group level.

One important opportunity provided by MVPA methods is *cross-classification* (Kaplan, Man, & Greening, 2015). Here, a classifier is trained on one experimental condition, and then tested on a different, independent experimental condition. Cross-classification can be used to control for potential confounds in MVPA. If for instance task difficulty is thought to affect task representations (Todd et al., 2013), a classifier can be trained to discriminate tasks in easy trials only, and its performance can then be tested on data from difficult trials only. If a brain region is affected by task difficulty and uses different spatial patterns to represent easy and difficult tasks, it will not be visible in this analysis. If however, a brain region is not affected by task difficulty and uses similar spatial patterns to represent easy and difficult tasks, the classifier can transfer the learned pattern differences from easy to difficult conditions, yielding significant results. Thus, cross-classification can be used to assess whether spatial activation patterns are invariant across different experimental conditions, making it an effective tool to avoid possible confounds (e.g. Reverberi et al., 2012b). Similarly, cross-classification can be used to test whether brain regions exhibit invariance with respect to *deliberate* experimental manipulations (Kaplan et al., 2015). For instance, cross-classification has been used to assess whether brain regions in the intentional control network use similar spatial patterns to represent freely chosen and externally cued intentions (Zhang et al., 2013). Any such identified brain region would represent intentions invariantly with respect to the free and cued conditions, suggesting that it has a general function in intentional control.

2.3 The neurobiological basis of fMRI response patterns

Several accounts have been put forward to explain the neural basis of the spatial patterns analyzed using MVPA (Haynes, 2015). The *biased sampling* account proposes that each voxel samples neurons organized into cortical columns (Bartfeld & Grinvald, 1992), e.g. orientation columns in early visual cortex (Hubel & Wiesel, 1968; Kamitani & Tong, 2005). Due to random fluctuations in the distribution of such columns, the number of columns sampled by each voxel will be slightly biased to contain more columns of one type relative to the other types. These voxel biases are too weak to be detectable in mass-univariate analyses, but MVPA is able to leverage the spatial distribution of multiple weakly biased voxels to detect information (Haynes & Rees, 2006). Biased sampling is best understood in visual cortex, but similar principles could explain task information in the PFC and parietal cortex. The PFC contains neurons that show task specific activity (Asaad et al., 2000; Kim & Shadlen, 1999), and these neurons are possibly distributed unequally across the cortex (Asaad, Rainer, & Miller, 1998). This might give rise to voxel biases similar to the ones observed in early visual cortex. Alternatively to biased sampling of cortical columns, it has been proposed that *macroscopic biases* at a larger spatial scale than cortical columns are the basis of MVPA signals (Freeman, Brouwer, Heeger, & Merriam, 2011; Freeman, Heeger, & Merriam, 2013), e.g. the *radial bias* effect in early visual cortex (Sasaki et al., 2006). Such large scale biases might give the false impression of sampling neuronal activity at the columnar level. Whether MVPA samples neuronal activity at the columnar level remains a debated issue (Alink, Krugliak, Walther, & Kriegeskorte, 2013), clearly requiring more research in this field.

3 Experiments

In this chapter, I will summarize the three experiments described in the dissertation. The complete manuscripts of the experiments can be found in the appendix. The first experiment investigated the interaction of intentional and motivational control processes in the brain (Wisniewski et al., 2014).

The second experiment investigated the neural correlates of task-reward-associations (Wisniewski et al., 2015). Finally, the third experiment investigated whether the intentional control network is functionally specialized with respect to freely chosen and externally cued intentions (Wisniewski et al., 2016).

3.1 Experiment 1: The neural basis of task choices in dynamically changing environments

Previous research investigating motivational effects on control processes largely focused on externally cued behavior (Etzel et al., 2015; Jiang & Xu, 2014; Kleinsorge & Rinkenauer, 2012; Woolgar et al., 2015). It thus remains unclear whether and how representations of freely chosen intentions and associated intentional control processes are affected by motivational processes. Furthermore, previous research investigating freely chosen intentions often let subjects decide between multiple highly similar options, with no evident reasons to choose one option over the other (Cunnington et al., 2002; Forstmann et al., 2006; Libet et al., 1983; Soon et al., 2008). In contrast, intentional control in real-life scenarios is often characterized by choosing behavior for specific reasons, like expecting it to lead to favorable outcomes. Both of these points highlight the need to study motivational and intentional control processes together, in order to test whether motivational effects observed on externally cued intentions generalize to freely chosen intentions and in order to increase the ecological validity of intentional control experiments.

In Experiment 1, subjects were given the free choice between one of three tasks in every trial. The environment changed dynamically while subjects performed the tasks, requiring them to constantly adapt to changing conditions. More specifically, subjects were instructed to identify a visual object on screen and determine its category (musical instruments, furniture, or means of transportation). The three tasks consisted of three different mappings of these categories on response buttons. Importantly, the difficulty of the three tasks varied independently, with the chosen task increasing in difficulty in each trial. Non-chosen tasks decreased their difficulty over time, and the longer a task

was not performed, the easier it would become. Task difficulty was varied by adding or subtracting random Gaussian noise to the pictures presented on screen. This procedure was similar to previous studies on foraging behavior, where the outcomes also changed dynamically on a trial-by-trial basis (Calhoun & Hayden, 2015; Kolling, Behrens, Mars, & Rushworth, 2012; Wilke, Hutchinson, Todd, & Czienskowski, 2009). The goal in this task was to minimize the errors committed over the whole experiment, and it was up the subjects to develop and implement a strategy to reach that goal. Behavioral results demonstrated that subjects committed more errors in highly difficult trials, and minimizing difficulty was thus a viable strategy to keep the error rate low. Importantly, difficulty motivated subjects' free choices in this experiment, by leading to different outcomes for different choice options. Subjects could either stay and perform the same task repeatedly (if the task was still easy), or could switch to performing a different task (if the current task became too hard). Behavioral results confirmed that subjects indeed followed this strategy. Additionally, changes in difficulty partly depended on subjects' choices, e.g. only the chosen task increased in difficulty. By making difficulty changes contingent on choices, subjects were given the opportunity to partly control changes in difficulty over the course of the experiment. This allowed subjects to have a much richer interaction with their environment than in previous experiments where choice outcomes changed over time, but subjects had no influence on these changes (Boorman et al., 2009; Hampton & O'Doherty, 2007).

Two independent searchlight MVPAs were performed. First, brain regions encoding task choices in local spatial activation patterns were identified. Second, brain regions encoding the current task difficulty, the major motivational variable affecting task choices, were identified. These two variables were highly correlated in behavior, but the two MVPAs were orthogonalized in order to independently assess the neural correlates of free choices and task difficulty. Results indicated that task choices were encoded in the right dmPFC and dACC. The task difficulty was encoded in a wide-spread network including the lateral and medial PFC, and the occipital cortex. In the next step, it was assessed which brain regions might mediate the effect of task difficulty on free task choices. One necessary (albeit not sufficient) condition for any such brain region is that it has to have access to

information about both choices and task difficulty. A conjunction analysis was thus performed, testing which brain regions encoded both task choices and the current task difficulty. Only the right dmPFC/dACC was identified, suggesting that only this brain region had access to the information necessary to mediate motivational effects on intentional control.

These results highlight the role of the dACC and dmPFC in both motivational and intentional control of behavior. They are consistent with previous work on effort-based motivational control (Botvinick et al., 2009) as well as predictions of the EVC theory (Shenhav et al., 2013), which postulates that the dACC weighs the benefit of choosing a task (lower difficulty) with the cost of exerting control over behavior (switching to a different task). Results from Experiment 1 show that the dACC contains information about whether subjects will switch to a different task or not, as well as the motivational variable leading to that choice, supporting this notion. Our results further support the WWW theory of intentional action in showing that the dmPFC is involved in *what* decisions (Brass et al., 2013). Complementary evidence for the central role of the dACC/dmPFC in mediating motivational effects on intentional control comes from the connectivity pattern of the dACC. It receives inputs from subcortical motivational control regions and projects to lateral prefrontal cognitive control regions (Pessoa, 2009; Rushworth, Noonan, Boorman, Walton, & Behrens, 2011), making it likely that information about both task choices and the motivational variables affecting them can be found in the dACC.

Despite being in line with these theories of intentional and motivational control, results should be interpreted with care. Given that subjects freely chose tasks in a complex environment, many different cognitive processes possibly contributed to these choices, e.g. uncertainty processing (Rushworth & Behrens, 2008; Volz, Schubotz, & von Cramon, 2003), conflict monitoring (Botvinick et al., 2001), or cost-benefit evaluation (Kennerley, Dahmubed, Lara, & Wallis, 2009; Walton, Bannerman, Alterescu, & Rushworth, 2003). All of these processes are associated with either the dmPFC or dACC, creating a reverse inference problem (Poldrack, 2006). From these results alone it remains difficult to specify which precise function the dACC/dmPFC fulfills. In Experiment 2, one key

process likely underlying observed task choices was investigated directly: associating tasks with their outcomes.

3.2 Experiment 2: The neural basis of task-reward-associations

In order to choose tasks with the highest possible outcome, we first need to learn and update associations between tasks and their outcomes. Once an association is learned, it can be used to choose tasks which maximize outcomes (Boorman et al., 2009; Hampton & O'Doherty, 2007; Koch et al., 2008). In dynamic environments, such as in Experiment 1, task-outcome-associations need to be continuously updated, as outcomes will change over time. Previously, it has been difficult to study the neural correlates of task-outcome-associations, due to the fact that their signals are often confounded with preparatory processes. Reward outcomes have reliable effects on task preparation (Jiang & Xu, 2014; Müller et al., 2007), bias choices towards the most rewarding option (Boorman et al., 2009), and affect neural task representations (Etzel et al., 2015). As soon as subjects associate a task with its outcome, they will start preparing for task execution and will expect to gain a reward, for instance by increasing attention to rewarding stimuli (Kahnt et al., 2014; Peck et al., 2009). These preparatory processes mask the neural signals correlated with merely associating a task with its outcome.

In Experiment 2, a reward-based modified delayed intention task was used (Haynes et al., 2007; Momennejad & Haynes, 2012) in order to isolate the neural signature of task-reward-associations. In each trial, subjects performed one of two tasks, either judging the parity or the magnitude of a number presented on screen (Momennejad & Haynes, 2013). For fast and correct performance, subjects could receive either a high or a low reward. Tasks and rewards were orthogonalized in this experiment. In the beginning of each trial, a "mapping cue" was presented. This cue contained information about the task-reward-association for both tasks that could potentially be performed in that trial. In half of the trials, subjects received this information: "If you are later asked to perform

the parity task, you can earn a high reward. But if you are later asked to perform the magnitude task, you can earn a low reward." In the other half of the trials, the task-reward-mapping was reversed. Importantly, subjects did not yet know which task they will later perform at this point in time, and needed to maintain the association of both tasks with their respective rewards. After a delay period, a "task cue" was presented, informing subjects about which task was to be performed in that trial. After another short delay, subjects saw the task screen and executed the instructed task for the specified reward. Importantly, before the onset of the task cue subjects could not prepare for the execution of the task, nor were they able to expect to gain a high or low reward. Information about the specific task and reward condition in each trial only became available after the task was specified in the task cue. Thus, between the mapping cue onset and the task cue onset, subjects could only represent the associations between both tasks and their respective outcomes, allowing us to isolate the neural signal of task-reward-associations. In order to ensure that only fMRI data from before the task cue onset entered the analysis, we combined MVPA and finite impulse response modeling (see Bode & Haynes, 2009; Soon et al., 2008 for more details).

Three independent MVPAs were performed, assessing the brain regions involved in representing tasks, rewards, and associations between both, respectively. Results indicated that task-reward-associations are represented in the bilateral inferior parietal cortex. The parietal cortex is known to be a part of the cognitive and intentional control network (Demanet, De Baene, Arrington, & Brass, 2013; Esterman et al., 2009; Pesaran et al., 2008; Sirigu et al., 2004), and it also plays a role in representing action values (Furl & Averbeck, 2011; Sugrue, 2004). These results provide direct evidence that the parietal cortex represents associations between tasks and their outcomes, which cannot be explained with other preparatory processes. Further analyses revealed that after the onset of the task cue, the same parietal regions also represent the task which was performed as well as the potential reward which could be gained. The same parietal brain region has thus been found to represent task-reward-associations *before* the onset of the task cue, and represent tasks and rewards

after the onset of the task cue. It essentially switches from representing one variable to representing other variables mid-trial.

This finding is in line with MD theory (Crittenden & Duncan, 2014; Duncan, 2010), which predicts the parietal cortex to be highly flexible to adapt to different task demands. Usually, support for the MD theory comes from studies that present subjects with highly different tasks separated in time (e.g. stroop, working memory, mental arithmetic, Fedorenko et al., 2013). Here, results demonstrate that at least a part of the MD network is capable of adapting to changing task demands on much shorter time-scales, within single trials. Similar results have been found before in nonhuman primates (Sigala, Kusunoki, Nimmo-Smith, Gaffan, & Duncan, 2008; Stokes et al., 2013), and current results extend these findings to humans using fMRI. Overall, the current results emphasize the flexibility of the parietal cortex in cognitive and motivational control. Interestingly, theories of intentional control (e.g. EVC or WWW theory) make no strong predictions about the parietal cortex, focusing instead on the role of the PFC.

Results from Experiment 2, which used reward as a motivational variable, are very different from those in Experiment 1, which used effort as a motivational variable. The dmPFC/dACC has been shown to mediate motivational effects on intentional control before, but seemingly plays no strong role in associating tasks with their outcomes. These associations are instead correlated with parietal cortex functioning. There are a number of differences in the experimental design that might have led to these divergent results. First, subjects freely chose tasks in a dynamically changing environment in Experiment 1. It is known that the dACC is most strongly involved if subjects are faced with novel situations, and dACC involvement decreases if tasks are performed routinely (Chein & Schneider, 2005; Koch et al., 2008). This possibly explains the lack of dACC results in Experiment 2, where the environment was not changing dynamically over time. Furthermore, the two experiments use two different motivational variables to motivate behavior, task difficulty and monetary rewards. It cannot be excluded that these two variables have different effects on control processes (Galea, Mallia, Rothwell, & Diedrichsen, 2015; Paschke et al., 2015). On the other hand, the PFC and parietal cortex

have been shown to interact tightly to support adaptive control of behavior (Polanía, Moisa, Opitz, Grueschow, & Ruff, 2015). Possibly the parietal cortex provides information about task-outcome-associations to the dACC to enable effective control (see General Discussion for more details, p. 38f.).

3.3 Experiment 3: The neural basis of freely chosen and externally cued intentions

Despite the fact that the regions constituting the cognitive and intentional control networks are well described (Badre & D'Esposito, 2009; Brass et al., 2005; Duncan, 2010; Koechlin, 2003; Ridderinkhof, Ullsperger, et al., 2004), the functional organization of this network remains highly debated (Crittenden & Duncan, 2014). On the one hand, gradient theories argue for functional specialization, especially within the PFC (Badre et al., 2009; Brass & Haggard, 2008; Koechlin & Summerfield, 2007; Venkatraman et al., 2009), while other theories argue for a generality of function (Stokes et al., 2013; Woolgar et al., 2015). A major problem in understanding the functional architecture of the intentional control network is the fact that global signal increases correlated with intentional control cannot be specifically attributed to intentional processes. They might equally reflect general preparatory processes correlated with intentional control, e.g. conflict resolution (Botvinick et al., 2001; Brass et al., 2013). MVPA studies somewhat alleviate this issue, as different intentions can be contrasted while preparatory processes can be kept constant. However, most previous MVPA studies on intentional control either investigated only externally cued intentions (Bode & Haynes, 2009; Gilbert, 2011; Woolgar et al., 2015), or only internally generated intentions (Haynes et al., 2007; Soon et al., 2008, 2013). In order to draw clear conclusions about the functional organization of the intentional control network, within-subject comparisons of free and cued intentions are needed. To date, few studies directly compared free and cued intentions within subjects (Bengtsson et al., 2009; Cunnington et al., 2002; Forstmann et al., 2005; Jahanshahi et al., 1995), especially investigating intention representations using MVPA (Zhang et al., 2013), and the functional organization of the intentional control network remains an open issue.

In Experiment 3, representations of intentions that were either freely chosen or externally cued were directly compared within-subjects. In each trial, subjects performed one of two different tasks, either adding or subtracting two numbers presented on screen (adapted from Haynes et al., 2007). Trials started with a cue presented on a screen. In half of the trials, the cue indicated that subjects could freely choose which of the two tasks to perform (*free condition*). In the other half of the trials, the cue indicated which of the two tasks was to be performed (*cued condition*). After a variable delay, subjects were presented two numbers on screen and executed the chosen or instructed task. This design allowed investigating which brain regions were specialized in representing only free or cued intentions, and which brain regions were involved in representing both. In order to first identify all regions containing information about any type of intentions, searchlight MVPA was used to discriminate between tasks collapsing across both free and cued trials. Results showed that the intentional control network was comprised of the left parietal cortex, and left lateral prefrontal cortex including the inferior frontal gyrus, middle frontal gyrus and premotor cortex. This result largely replicates previous findings identifying a similar network (Bode & Haynes, 2009; Zhang et al., 2013). In order to test whether this network plays a general role in representing both free and cued intentions, a classifier was trained to discriminate freely chosen tasks and tested on externally cued tasks. Only brain regions using similar spatial patterns for free and cued tasks survived this cross-classification procedure (Kaplan et al., 2015). Any such region is likely having a general function in representing intentions, as representations are independent of the way the intentions were formed (free or cued). In a whole brain analysis, the left ventral premotor cortex and left inferior frontal gyrus were found to use similar spatial patterns to represent freely chosen and externally cued intentions. A more sensitive ROI analysis revealed that every brain region which was a part of the intentional control network (left lateral PFC and parietal cortex) used similar spatial patterns to represent freely chosen and externally cued intentions. This suggests that the lateral PFC and parietal cortex have a general function in representing different types of intentions, showing no strong functional specialization.

Results from Experiment 3 are largely in line with predictions from the MD theory (Duncan, 2010), showing that both the parietal and lateral prefrontal cortex have a general function in representing both free and cued intentions. Results do not directly contradict gradient theories however. For instance the WWW theory proposes a gradient along the medial wall of the PFC (Brass et al., 2013). Given that no results in the medial PFC were found, no strong conclusions about the organization of this region can be drawn. The reason for the absence of medial PFC results is likely the fact that especially the dACC is mostly involved in performing novel tasks and its involvement decreases with increasing routine (Chein & Schneider, 2005). Subjects underwent an extensive training session, and this might have reduced dACC involvement in our task. Nevertheless, results are more in line with the MD theory than with theories arguing for functional specialization of the fronto-parietal control network.

Furthermore, this experiment only assessed whether the intentional control network is functionally specialized with respect to the free or cued formation of intentions. Although no specialization for this factor was found, this clearly does not rule out the possibility that the network is functionally specialized with respect to other variables which were not investigated here. For instance, regions involved in maintaining intentions might differ when cognitive load is high during their maintenance, as compared to low cognitive load during their maintenance (Momennejad & Haynes, 2013).

4 Conclusions and Outlook

4.1 Motivational influences on intentional control in the brain

Intentional control of behavior is a fundamental part of human behavior. Our environment rarely is kind enough to provide clear instructions for every-day problems, creating the need for internal control of behavior. Previous research identified a fronto-parietal network supporting intentional control (Brass et al., 2013; Forstmann et al., 2006; Soon et al., 2013; Zhang et al., 2013). These

control processes have been found to be affected by motivational processes, with rewards leading to improved self-control (Boehler et al., 2012), task reconfiguration (Jiang & Xu, 2014), and conflict resolution (Dreisbach & Fischer, 2012). Rewards have further been found to affect task representations in the fronto-parietal cortex (Etzel et al., 2015). Candidate regions possibly mediating such motivational effects on intentional control are the dACC (Holroyd & Yeung, 2012; Pessoa, 2010; Shenhav et al., 2013) and parietal cortex (Etzel et al., 2015; Louie et al., 2011; Woolgar et al., 2015). The results described in this thesis provide novel evidence supporting both the role for the dACC as well as parietal cortex in mediating motivational effects on intentional control.

In Experiment 1, subjects freely chose between three different tasks in each trial, with task difficulty changing dynamically on a trial-by-trial basis. Behavioral results indicated that free choices were indeed motivated by the changing task difficulties. In previous work on the neural basis of *intentional* control, it often remained unclear on which grounds subjects made their choices, as the choice options were highly similar and there were no clear reasons to favor one option over the other (Arrington & Logan, 2004; Forstmann et al., 2006; Libet et al., 1983; Soon et al., 2008; Zhang et al., 2013). In Experiment 1 on the other hand, subjects' choices were clearly motivated through the dynamically changing environment. In previous work on motivational effects on *cognitive* control, subjects were often externally cued on which tasks to perform in each trial (Dreisbach & Fischer, 2012; Etzel et al., 2015; Jiang & Xu, 2014). Although this research demonstrated that control of externally guided behavior is modulated by motivational processes (Chiew & Braver, 2014; Kleinsorge & Rinkenauer, 2012; Locke & Braver, 2008), it remained unclear whether the same is true for more internally guided behavior. In Experiment 1, subjects freely chose which tasks to perform in each trial, allowing the investigation of motivational effects on internally guided behavior. MVPA results demonstrated that the dACC and dmPFC were the only brain regions with access to information about the choice ("what") and the factor motivating that choice ("why"). This suggests that these brain areas play a key role in mediating motivational effects on freely chosen behavior, extending previous findings on their importance for both motivational and cognitive control (Bush et al., 2002;

Rushworth & Behrens, 2008; Shima & Tanji, 1998; Walton et al., 2007). For instance, the dmPFC and dACC have been shown to represent freely chosen tasks (Haynes et al., 2007), as well as negative prediction errors (Boorman, Rushworth, & Behrens, 2013; Hauser et al., 2015), a signal encoding expected action costs. Results from Experiment 1 follow a similar pattern. Furthermore, the dACC is ideally connected to mediate motivational and intentional control processes (Kennerley et al., 2006; Pessoa, 2010; Williams et al., 2004). Results are compatible with the notion that value signals are transferred to the dACC from subcortical brain regions (Balleine & Ostlund, 2007; Kahnt, Park, et al., 2012; Schultz, 2013). The dACC then might use this information to compute a signal weighing the costs and benefits of choosing a task (Shenhav et al., 2013), then transferring this signal to brain regions implementing control (dlPFC) and controlling action (motor cortex, Hare, Schultz, Camerer, O'Doherty, & Rangel, 2011).

In Experiment 2, subjects associated different tasks with their reward outcomes, while these associations changed on a trial-by-trial basis. Here, results highlight the role of the parietal cortex. It first represented associations between tasks and their outcomes, switching mid-trial to representing the tasks and outcomes directly. The parietal cortex thus switches flexibly between representing three different variables, at each point in time representing the aspect of the task most relevant to the subject. Associating tasks with their outcomes clearly is a key function enabling task choices in Experiment 1. However, this function could not be investigated directly in the previous experiment and Experiment 2 was designed to explicitly investigate this function.

Previous results demonstrated that the parietal cortex is an important part of the cognitive control network (Esterman et al., 2009; Shomstein, 2012) and is causally linked to intentional control (Sirigu et al., 2004). The parietal cortex is further known to represent action values (Dorris & Glimcher, 2004; Platt & Glimcher, 1999; Sugrue, 2004), and thus has a role in both intentional and motivational control. Results from Experiment 2 now directly demonstrate that the parietal cortex also represent associations between tasks and their outcomes, further strengthening its role in motivational and cognitive control (Polanía et al., 2015). This is especially interesting since the parietal cortex has not

been in the focus of many theories on cognitive or intentional control. Instead, most theories focus on describing the role of the dACC (Botvinick, 2007), medial PFC (Brass et al., 2013), or lateral PFC (Badre & D'Esposito, 2009; Koechlin, 2003). Theories of motivational effects on cognitive control focus on similar regions, especially the dACC (Shenhav et al., 2013), and medial PFC (Kouneiher et al., 2009). Contributions of parietal cortex remain poorly understood, however.

Addressing this issue, the information flow in the brain during value-based choices has received increased attention recently (Hare et al., 2011; Kubanek & Snyder, 2015). The dmPFC and parietal cortex are thought to receive value information which is projected from regions in the vmPFC and then compare the values of different choice options (Hare et al., 2011). The same study shows that both regions then connect to the motor cortex to implement the chosen option. Both the medial PFC and parietal cortex are thus critical for transforming stimulus values into motor behavior. Furthermore, in order to successfully do so, activity in the PFC and parietal cortex needs to be coupled and phase locked, as a disruption of the phase coupling of PFC and parietal cortex leads to less accurate value-based choices (Polanía et al., 2015). Results from the first two experiments can be used to tentatively expand this theory of information flow. Experiment 2 is compatible with the notion that the parietal cortex receives value information from the vmPFC, and then maps the value onto specific tasks. Experiment 1 has shown that the dmPFC/dACC contains information about both task choice and the motivational variables driving these choices, likely weighing the costs and benefits of exerting control over behavior (Shenhav et al., 2013). Information about the current task-outcome-associations is necessary for this computation, which might be provided to the dACC from the parietal cortex. A disturbance in this information transmission will impair the ability of the dACC to weigh the costs and benefits of controlling behavior, and will lead to impairments in performance (as was evident in Polanía et al., 2015). The results described in experiments 1 and 2 therefore extend this theory of cortical information flow during choice behavior by assigning different functional roles to the dACC/dmPFC and parietal cortex, respectively.

4.2 The functional organization of the intentional control network

Although the brain regions constituting the cognitive and intentional control network are fairly well described, the functional organization of this network remains debated. Whereas some theories argue for a strong functional specialization, especially in the prefrontal cortex (Badre & D'Esposito, 2009; Brass et al., 2013; Koechlin, 2003), other theories argue for functional generality (Cole et al., 2013; Duncan, 2010; Fedorenko et al., 2013). These opposing theories draw different pictures of the neural basis of cognitive and intentional control. On the one hand, one might argue that heterogeneous cognitive control functions are supported by a modular neural architecture, with different brain regions playing different parts in behavioral control (Badre & D'Esposito, 2009). On the other hand, one might argue that control functions are supported by "general purpose" brain regions, which are able to flexibly adapt their functions to current environmental demands (Duncan, 2010). Despite proposing contrary views of cognitive control, these accounts are not strictly mutually exclusive. Possibly a core set of brain regions are able to reconfigure theory functions to meet current demands (Woolgar et al., 2015), while brain regions outside this brain network have more specialized functions (Dosenbach et al., 2007). For instance, the SMA might be a multiple demand region (Fedorenko et al., 2013), but this does not exclude that neighboring, more anterior medial prefrontal regions have specialized functions (Venkatraman et al., 2009).

In Experiment 3, the representations of free and cued intentions were directly compared, investigating whether the intentional control network is functionally specialized with respect to this variable. It was thus tested whether this difference in the conditions under which intentions were formed affected their representations, or whether intention representations were invariant. Results demonstrated that a left lateralized network including the lateral PFC and parietal cortex encoded which task subjects intended to perform. Interestingly, these regions were found to encode tasks using similar spatial patterns in both freely chosen and externally cued conditions. This seems to suggest that the left lateral PFC and parietal cortex have a general role in representing intentions (Kaplan et al., 2015), using a spatial code that is independent of the way the intentions were formed.

This result is more in line with the MD theory (Duncan, 2010), in that it shows that the fronto-parietal network identified in our experiment shows functional generality with respect to freely chosen vs. externally cued intentions, using similar spatial patterns to encode both types of intentions. Note however, that this result provides no direct evidence against some functional specialization theories. For instance Dosenbach et al. (2007) suggested that the cognitive control network can be subdivided into a fronto-parietal and a cingulo-opercular sub-network. The authors then argue that the fronto-parietal sub-network is involved in adaptive trial-by-trial control, while the cingulo-opercular sub-network is involved in sustained control processes. All brain regions identified in our experiment fall into the fronto-parietal sub-network and thus might reflect the need for adaptive control processes during task performance. None of the identified brain regions falls into the cingulo-opercular sub-network, making it difficult to draw conclusions about the relative role of these two sub-networks. Results do suggest however, that there is no strong functional specialization with respect to free and cued intentions within the fronto-parietal network (in contrast to Zhang et al., 2013), and that this network thus might have a general role in intentional control.

Experiments 1 and 2 further provide complementary evidence for the functional generality of brain regions associated with cognitive and intentional control. Experiment 1 showed that the dACC/dmPFC is part of both the intentional control network as well as the motivational control network, suggesting it is not specialized in either intentional or motivational control processes. Experiment 2 showed that the parietal cortex encodes associations between tasks and rewards, as well as tasks and rewards per se. Again, this shows that the parietal cortex is not functionally specialized to either cognitive or motivational control. Taken together, these results suggest that the identified regions, including dACC/dmPFC, parietal cortex, as well as lateral PFC, have a general function in intentional and motivational control, at least with respect to the experimental manipulations used. Of course, it cannot be ruled out that they are specialized along other, untested dimensions, or that other brain regions show stronger functional specialization, either at the level of

individual brain regions (Venkatraman et al., 2009), or at the network level (Dosenbach et al., 2007). More research is needed to resolve these open issues.

4.3 Open questions and future directions

The three experiments presented in this dissertation can only form a starting point for a systematic investigation into the neural basis of motivated intentional control and its functional organization. Although the experiments do address some issues in the literature, many open questions remain that warrant further investigation.

One important open issue is identifying and isolating the processes underlying complex adaptive behavior, including the contributions of intentional and motivational processes. In order to understand adaptation to dynamically changing environments, such as was observed in Experiment 1, we must gain an understanding which specific cognitive processes support such adaptive behavior. This thesis adopted the strategy of carefully designing follow-up experiments isolating and investigating single processes which are thought to subserve complex control functions. For this reason, task-reward-associations were investigated in Experiment 2. A complementary approach is to use cognitive modeling and apply it to fMRI (Forstmann & Wagenmakers, 2015). The limited information contained in commonly used behavioral measures of control functions (such as RTs and choices), has made it difficult to gain a more mechanistic understanding of the control processes involved in intentional and cognitive control. It can therefore be useful to model behavior first and then assess the neural correlates of estimated latent variables (O'Doherty, Hampton, & Kim, 2007). For instance, *reinforcement learning* is used routinely to infer trial-by-trial prediction errors from subjects' behavior (Botvinick, 2012; Frank et al., 2015; Shteingart & Loewenstein, 2014). By using model predictions and incorporating them into general linear models of fMRI data, one can investigate the neural basis of prediction errors, which are not directly observable in behavioral data alone (O'Doherty et al., 2007).

An alternative model class which gained much popularity over the last years are *drift diffusion models* (Ratcliff & McKoon, 2007). In DDMs, a decision process is modeled as a stochastic process accumulating evidence over time until the gathered evidence crosses a decision boundary (for a critical discussion see Latimer, Yates, Meister, Huk, & Pillow, 2015). DDMs have been used successfully to model the behavioral and neural effects of perceptual decision processes (Heekeren, Marrett, & Ungerleider, 2008), or speed-accuracy tradeoffs in behavior (Forstmann et al., 2011; Wenzlaff, Bauer, Maess, & Heekeren, 2011) in terms of gathering of sensory evidence. They have further been shown to provide accurate descriptions of value-based choice processes (Basten, Biele, Heekeren, & Fiebach, 2010), suggesting that value information is accumulated in the brain stochastically over time, similar to sensory evidence (Krajbich & Rangel, 2011). For instance, Experiment 1 suggested that difficulty-based choices rely on the dmPFC/dACC. In future experiments, DDM could be used to illuminate the computational role of this brain region during decision-making in dynamically changing environments (see also Hunt et al., 2012). Both, reinforcement learning and DDMs have the power to provide a more mechanistic understanding of complex control processes, as well as linking behavioral findings more closely to the observed neural effects[4].

A second open issue concerns the difference between effects of rewards vs. effects of effort on intentional control. In Experiment 1, intentional control was motivated by task difficulty, while in Experiment 2, control was affected by monetary rewards. While the dACC subserved control in Experiment 1, only the parietal cortex was correlated with control in Experiment 2. This divergence of results might stem from a number of differences in experimental design, but one likely candidate is the variable used to motivate behavior. It has been shown previously that gains and losses differentially affect attentional control processes (Paschke et al., 2015), as well as motor adaptation (Galea et al., 2015). A similar pattern might be in place for intentional control, with rewards and effort having different and dissociable effects (see also Botvinick et al., 2009; Croxson et al., 2009). In future experiments, the effects of rewards and effort thus have to be directly contrasted, in order to

[4] To see how a different framework, dynamic systems theory, can be used to model decision processes, see Deco, Rolls, & Romo, 2009 and Scherbaum, Dshemuchadse, & Kalis, 2008.

test for possible dissociations. This might then help explain the observed differences in results between Experiments 1 and 2.

A third open issue is identifying more variables along which the intentional control network might be functionally specialized. Results from Experiment 3 seem to support the functional generality of the fronto-parietal control network with respect to the way intentions were formed (freely chosen vs. externally cued). These results provide no direct evidence for or against functional specialization in regions outside of the network identified (lateral PFC, parietal cortex). They neither provide evidence against functional specialization according to other factors which were not tested, such as the amount of cognitive load present during intention maintenance (Momennejad & Haynes, 2013). In order to resolve the issue of functional specialization of the intentional control network, further studies which systematically assess the effects of multiple different influences on intention selection, maintenance, and implementation (Dumontheil, Gilbert, Frith, & Burgess, 2010; Tsujimoto, Genovesio, & Wise, 2008) are clearly needed.

Lastly, the results provided here only assessed information about intentions in local spatial activation patterns in the brain. This does not exclude that information about intentions might also be stored at different levels, e.g. in the pattern of inter-regional correlations of BOLD time-courses (Gilbert, 2011), which can be assessed using graph theory (Cole et al., 2013; Dosenbach et al., 2007; Kouneiher et al., 2009). Analyses at the network level might identify information about intentions that is undetectable in local spatial activation patterns.

4.4 Concluding summary

The aim of this thesis is to take a step forward in investigating the neural correlates of intentional control. The first broad research question addressed the interaction of motivational and intentional control processes. In particular, Experiment 1 assessed whether and how motivational control processes affect freely chosen behavior, showing that the dACC/dmPFC are likely playing a key role in

mediating such effects. Moreover, Experiment 2 assessed the neural basis of task-reward-associations that underlie intentional control of behavior. Here, the parietal cortex was found to play a critical role in representing associations between tasks and their outcomes. Both findings substantially expand our knowledge and theories of motivational and intentional control. The second broad research question aimed to shed light on the functional organization of the intentional control network. The current results suggest that the intentional control network shows no strong internal functional specialization with respect to free vs. cued intention formation, instead supporting its functional generality. These results inform the current debate on the degree of functional specialization in the cognitive and intentional control network. Overall, the results presented in this dissertation contribute to current debates on the neural basis of intentional control, and provide a promising starting point for further systematic investigations of this central trait of human behavior.

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6 Supplements

A Publications

First author or equal contribution (*) in peer-reviewed journals

Wisniewski, D.*, Reverberi, C.*, Tusche, A., & Haynes, J.-D. (2014). The Neural Representation of Voluntary Task-Set Selection in Dynamic Environments. *Cerebral Cortex*. http://doi.org/10.1093/cercor/bhu155

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Tusche, A., Kahnt, T., **Wisniewski, D.**, Haynes, J.-D. (2013). Automatic Processing of Political Preferences in the Human Brain. *NeuroImage,* 72, 174–82.

Conference Talks

Wisniewski D. 2012. Predicting decisions in a dynamically changing environment from activation patterns in the dorso-medial prefrontal cortex, *2nd Einstein Fellowship Symposium on "Decision-making"*, Berlin

B Research Articles

This thesis encompasses three studies. For full texts, please follow the respective links.

Experiment 1

Wisniewski, D., Reverberi, C., Tusche, A., & Haynes, J.-D. (2014). The Neural Representation of Voluntary Task-Set Selection in Dynamic Environments. *Cerebral Cortex, bhu155*. http://doi.org/10.1093/cercor/bhu155

[Full Text]

Experiment 2

Wisniewski, D., Reverberi, C., Momennejad, I., Kahnt, T., & Haynes, J.-D. (2015). The Role of the Parietal Cortex in the Representation of Task–Reward Associations. *The Journal of Neuroscience*, *35*(36), 12355–12365.

[Full Text]

Experiment 3

Wisniewski, D., Goschke, T., & Haynes, J.-D. (2016). Similar coding of freely chosen and externally cued intentions in a fronto-parietal network. *NeuroImage*, 134, 450-458, 10.1016/j.neuroimage.2016.04.044.

[Full Text]

C Selbstständigkeitserklärung

Ich erkläre, dass ich die vorliegende Arbeit selbstständig und nur unter Verwendung der angegebenen Literatur und Hilfsmittel angefertigt habe.

Berlin, den 16.12.2015 David Wisniewski